IJM 6: 1–27 (2011)
doi: 10.3897/ijm.6.1949
www.pensoft.net/journals/ijm

RESEARCH ARTICLE

A peer-reviewed open-access journal
INTERNATIONAL JOURNAL OF
Myriapodology

Trans-segmental serial colour patterns in millipedes and their developmental interpretation (Diplopoda)

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Academic editor: *R. Mesibov* | Received 23 August 2011 | Accepted 27 September 2011 | Published 20 December 2011

Citation: Enghoff H (2011) Trans-segmental serial colour patterns in millipedes and their developmental interpretation (Diplopoda). In: Mesibov R, Short M (Eds) Proceedings of the 15th International Congress of Myriapodology, 18–22 July 2011, Brisbane, Australia. International Journal of Myriapodology 6: 1–27. doi: 10.3897/ijm.6.1949

Abstract

Trans-segmental serial colour patterns, i.e., colour patterns consisting of repeated elements, each of which covers several diplosegments / body rings, are described from several millipede taxa: *Centrobolus vastus* (Attems, 1934) var. *sexfasciatus* Lawrence, 1967 (Spirobolida: Pachybolidae), *Sagmatostreptus strongylopygus* (Attems, 1950) (Spirostreptida, Spirostreptidae), and several groups of the order Platydesmida. The occurrence of similar patterns in *Siphonocryptus zigzag* Enghoff, 2010 (Siphonocryptida, Siphonocryptidae) and unidentified species of the order Chordeumatida is recorded. The patterns are shown in most cases to correlate with postembryonic growth, anamorphosis, i.e., each pattern elements corresponds to a set of diplosegments added during a moult.

Keywords

Centrobolus, *Sagmatostreptus*, *Platydesmus*, *Pseudodesmus*, *Brachycybe*, *Siphonocryptus*, *Australeuma*, *Schedotrigona*, anamorphosis, aposematic

Introduction

Millipedes have a general reputation of being discretely, not to say boringly coloured. There are, however, numerous exceptions, including such aptly named species as "the shocking pink dragon millipede" (Enghoff et al. 2007), "the emerald green giant millipede" (Wesener and Schütte 2010) and the "fire millipedes" of Madagascar

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(Wesener et al. 2009). Further examples of colourful millipedes are European pill millipedes, genus *Glomeris* (Hoess 2000), giant pill millipedes of Madagascar, genus *Zoosphaerium* (Wesener 2009), and N American flatbacked millipedes of the family Xystodesmidae (Marek and Bond 2006). Plenty of colourful millipede photos can also be found on Flickr Hive Mind (http://fiveprime.org/flickr_hvmnd.cgi).

Millipedes may be uniformly coloured, or they may have more or less pronounced colour patterns. A very common pattern is one of transverse stripes, where each diplosegment is differently coloured on its front and hind parts. Instead of transverse stripes, there may be one or more contrastingly coloured spots on each diplosegment, or there may be one or more continuous longitudinal bands along the body.

Most millipedes have defensive glands secreting such repellant substances as hydrogen cyanide or benzoquinones (Eisner et al. 1978, Shear et al. 2007), and strong and/or contrasting colouration in millipedes certainly has an aposematic function. Thus, strongly coloured species tend to occur in more open places and/or to be more diurnal, than their drab relatives (e.g., Lawrence 1967). Strongly coloured/patterned millipedes take part in mimetic relationships with one another (Whitehead and Shelley 1992, Marek and Bond 2009), with lizards (Vitt 1992) or even with spiders (Levi 1965).

Many millipede species have segmentally repeated colour patterns, e.g., contrastingly coloured paranota as in numerous species of Polydesmida. In some cases, the series is discontinous, for example in the European polydesmid *Polydesmus collaris* C.L. Koch. 1847, in which the paranota of body rings 4, 6, 8, 11, and 14 (i.e., the rings which do not carry ozopores) are contrastingly yellow on a dark brown background (Korsós et al. 2001: fig. 1, Kime and Enghoff 2011: fig. 9, several websites including http://www.naturefg.com/pages/c-animals/polydesmus%20collaris.htm), or the West African chelodesmid *Prepodesmus ornatus* (Peters, 1864) in which the body rings *with* ozopores (5, 7, 9–10, 12–13, 15–18) have contrasting light spots (Attems 1938a: 373).

In a few cases, the colour pattern consists of repeated elements, each of which covers several diplosegments / body rings. These "trans-segmental serial colour patterns" are the subject of the present paper. The study was prompted by the discovery of *Siphonocryptus zigzag* Enghoff, 2010.

Material and methods

Specimens were examined from the following collections: MRAC: Muséum Royal d'Afrique Centrale, Tervuren, Belgium. ZMUC: Natural History Museum of Denmark (Zoological Museum), University of Copenhagen, Denmark. Further information was extracted from images kindly provided by colleagues and/or found on the internet.

Interpretation of postembryonic development in *Centrobolus* and *Sagmatostreptus* is based on the 'law of anamorphosis' (Enghoff et al. 1993). It should be borne in mind that when speaking of 'segments' in millipedes, many authors refer to the obvious body divisions which are in fact mostly diplosegments. To avoid ambiguity, Enghoff

et al. (1993) recommended using 'body ring' in those groups (such as Spirobolida and Spirostreptida) where the terga, pleura and sterna constituting a diplosegment are all fused, ''pleurotergite' in those groups (such as Siphonocryptida, Platydesmida and Chordeumatida) where the sterna remain free, and 'tergites' in groups where also the pleura remain free. This terminology will be adhered to here.

Centrobolus vastus (Attems, 1934) var. *sexfasciatus* Lawrence, 1967 – a simple case

Several species of the South African genus *Centrobolus* (Spirobolida: Pachybolidae) are bright red in colour or have a striking red-black colour pattern. In one taxon, the colour pattern is of the trans-segmental type, i.e., *C. vastus* (Attems, 1934) var. *sexfasciatus* Lawrence, 1967 (Figs 1–2, see also Lawrence 1967: fig 46). In this taxon, there are six transverse black bands on a bright red background, each transverse band covering two successive body rings.

I have examined five males and five females collected at Port St. Johns, Eastern Cape, South Africa, date unknown, M. Boddely leg. (MRAC). This sample is very homogeneous: All specimens possess 43 podous body rings and have no apodous body rings in front of the telson, i.e., they have the body ring formula 43+0+T sensu Enghoff et al. (1993). In all ten specimens, the black transverse bands occur on body rings 17–18, 22–23, 27–28, 32–33, 37–38 and 41–42 (the bands are indistinct on body rings 17, 22, 27, 32, 37 and/or 41 in 3 specimens and also on ring 33 in two specimens. The specimen in Fig. 1 has the black bands on exactly the same body rings as the ones I have seen, as well as the one depicted by Lawrence (1967).

Functionally, this pattern can intuitively be interpreted as aposematic (Lawrence 1967), but how is the pattern developed during the ontogeny of *C. vastus* var. *sexfasciatus*?

Like at least most other members of the order Spirobolida, *Centrobolus* species develop postembryonically through a process known as hemianamorphosis: During the first several moults (the anamorphic phase), new body rings and leg-pairs are added until a (still immature) stadium in which the adult number of body rings and leg-pairs is reached, whereafter further moults take place without the addition of body rings and leg-pairs (the epimorphic phase). During the anamorphic phase, there is a number of legless (apodous) body rings in front of the telson, and according to the so-called 'rule of anamorphosis', the legless body rings turn leg-bearing (podous) after the next moult. (The existence of mature specimens with apodous rings in a few spirobolidan species [Enghoff et al. 1993: 199] suggests that in these, euanamorphosis rather than hemianamorphosis takes place.) See Enghoff et al. (1993) for more information on anamorphosis. No direct observations on the postembryonic development of *Centrobolus* species have been published, but something can be inferred from numbers of podous and apodous body rings in various species of the genus published mainly by Schubart (1966), but also by Jeekel (1958), see Table 1. Some of the body ring formulae in the table form a sequence leading to the epimorphic number of body rings (43+0+T) ob-

Figure 1. *Centrobolus vastus* var. *sexfasciatus* photographed by Guido Coza at Port. St. Johns, Eastern Cape, South Africa. See also http://www.flickr.com/photos/46608040@N04/5261677348/ (under *C. fulgidus*).

served in *C. vastus* var. *sexfasciatus*. This series of anamorphic stadia resembles what one sees in other spirobolidans in terms of body ring increments between stadia (Table 2). If the podous body ring numbers in this sequence (21, 26, 31, 36, 40) are plotted on an adult specimen (Fig. 2) it is seen that these podous rings are all just in front of one of the transverse black bands. It would therefore seem that the black bands are formed in connection with anamorphic moults and that they occupy the first two of the newly formed podous body rings.

The trans-segmental colour pattern in *C. vastus* var. *sexfasciatus* can thus be explained as a consequence of anamorphic development. This kind of pattern remains, as far as known, unique with the Spirobolida.

Sagmatostreptus strongylopygus (Attems, 1950) – a more complicated case

In the east African spirostreptid *Sagmatotreptus strongylopygus* (Attems, 1950) the body is generally light brown, but in the central and posterior part a blackish pattern of 6–7 elements occurs (Hoffman and Enghoff 2011). Each element consists of 3–4 body rings with a mid-dorsal black marking, the markings becoming broader towards the tail end such that each set of marked body rings appears triangular (Fig. 3). The sets of marked body rings are separated by two unmarked body rings. Table 3 gives details of the colour pattern in 26 specimens of *S. strongylopygus*. Although there is some variation, there is a clear tendency for the black markings to occur, in sets of 1–4 rings, on

Table 1. Anamorphic specimens of *Centrobolus* spp. recorded by Schubart (1966) and Jeekel (1958). The formulae give number of podous body rings + number of apodous body rings + T (=telson). The last column gives the known formulae (based on Schubart 1966) of *Centrobolus* specimens having reached the epimorphic stage. Formulae which follow from one another according to the 'law of anamorphosis' are connected with arrows.

							Epimorphic
6+10+T				31+4+T →	35+4+T →	39+3+T →	42+0+T
6+12+T		21+5+T →	26+5+T →	31+5+T →	36+4+T →	40+3+T →	43+0+T
			28+5+T		37+4+T →	41+3+T →	44+0+T
		23+6+T					45+0+T
	20+5+T						

Table 2. Numbers of apodous body rings in the last seven anamorphic stadia of pachybolid millipedes. Data from the compilation by Enghoff et al. (1993) (1), Dhaenens & VandenSpiegel (2006) (2), and Enghoff (2011) (3).

Species	**No. of podous rings in epimorphic spms**	**No. of apodous rings in last six anamorphic stadia**						**Ref.**
Dactylobolus bivirgatus (Karsch, 1881)	35–39	4–5	4–5	4–5	4	3–4	2	1
Pelmatojulus ligulatus (Voges, 1878)	54–55	6	6	6	6	5	3	1
Pelmatojulus insignis Saussure, 1860	53–56	5–6	5–6	5–6	5–6	4–5	3	1
Epibolus pulchripes (Gerstäcker, 1873)	51–54	6	6	6	6	5	3	2
Crurifarcimen vagans Enghoff, 2011	56	6	6	6	6	5	3	3

body rings 22–24, 27–30, 32–34, 36–39, 42–43 and 45–47, with scattered occurrences between as well as behind these intervals.

The relatively few anamorphic specimens (e.g., Fig. 4) studied provide a clue to the significance of the patterns: The anamorphic specimen with 29 podous + 5 apodous body rings would, according to the 'law of anamorphosis' (cf. above under *Centrobolus vastus* var. *sexfasciatus*) give rise to a specimen with 34 podous rings. This specimen has black markings on rings 28–29, i.e., the two last podous rings, and just under half (11 out of 25) of the larger specimens have a series of black markings ending on ring 34. The anamorphic specimens with 33–34 podous + 5 apodous rings would give rise to individuals with 38–39 podous rings in the next stadium, and 16 out of 20 larger specimens have a series of black markings ending on ring 38 or 39. It thus seems that the posterior 1–4 out of a set of podous body rings acquired at a moult is distinguished by black markings. Using this 'key', the colour patterns can be translated into series of inferred body ring formulae for each specimen, see Table 4. In the table, the early stadia are denoted as "n RO" where RO stand for "rows of ocelli" – this is a common way to denote developmental stadia in millipedes because in many groups, one row of ocelli is added at each moult (Enghoff et. al. 1993). Counting rows of ocelli is easy on specimens with up to 34 podous body rings. Specimens with 35–44 podous rings are not represented in the available material, but in specimens with 45 or more podous rings, the ocellar rows are irregular and apparently 'too numerous': in those cases where

Figure 2. *Centrobolus vastus* var. *sexfasciatus*, female from Port. St. Johns, Eastern Cape, South Africa, date?, M. Boddely leg. (MRAC). The arrows point at the body rings which are the posteriormost podous rings in the inferred anamorphic stadia. N. Ioannou phot. Length of specimen 60 mm.

Figure 3. *Sagmatostreptus strongylopygus*, subadult female from Amani, E Usambara Mts., Tanzania, 11 April 1985, T.G. Nielsen leg. (ZMUC), dorsal and lateral views. N. Ioannou phot. Length of specimen 117 mm.

Figure 4. *Sagmatostreptus strongylopygus*, anamorphic juvenile from Amani, E Usambara Mts., Tanzania, 26 July 1974, I.B. Enghoff & H. Enghoff leg. (ZMUC), 34 podous + 5 apodous rings, 5 rows of ocelli. N. Akkari phot. Scale 2 mm.

rows can be discerned at all, there are at least 11 rows in specimens with 45+ podous rings although just 7 would have been expected in a specimen with 45 podous rings if *S. strongylopygus* followed the normal pattern of ocellar increments. (Maybe *S. strongylopygus* which leads a comparatively overt life, cf. Hoffman and Enghoff 2011, has particularly strongly developed eyes, hence the 'supernumerary' rows.)

The bewildering multitude of inferred and observed segment formulae is summarized in Table 5. The ranges of podous body rings in each inferred stadium are unoverlapping up to stadium 5RO+1.

Table 6 shows the most frequent inferred body ring increments during the transition from stadium n to stadium n+1.

Looking at the complete sequences, there are hardly two specimens with identical inferred sequences, although some come close:

23+5+T → 28+5+T → 33+5+T → 38+4+T → 42+4+T → 46+3–4+T: specimens ZMUC 00101338(1) and ZMUC 00101338(2), which have the epimorphic formula 51+0+T

23+5+T → 28+5+T → 33+5+T → 38+5+T → 43+4+T → 47+3/?+T. This pathway is followed by specimens ZMUC 00101344 (stadium 3RO missing) and ZMUC 00101374(1) which have the epimorphic formula 52+0+T

The inferrred course of anamorphosis in *S. strongylopygus* is consistent with that found in another spirostreptid, *Archispirostreptus tumuliporus* (Karsch, 1881) (= *Graphidostreptus t.)* (Gillon and Gillon 1982) which has a similar number of podous rings in the epimorphic stages. This lends credibility to the method of inference. Other spirostreptids for which data on anamorphosis are available (see Enghoff et al. 1993)

Table 3. Colour patterns in 26 specimens of *Sagmatosreptus strongylopygus*. "B" on a grey background indicates a clear black marking; "b" or "?" on a lighter grey background indicates indistinct and almost invisible markings; "a" on a yellow background indicates apodous body rings; "T" on a yellow background indicates the telson. No markings occur on body rings 1–20 on these specimens.

Collection no.	Spm no.	Sex	Rings	Ø (mm)	RO	No. of podous rings																																		
						20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	
ZMUC 00101372	1	F	53+0+T	12,4	?										B	B			B	B	B				B	B				b				b						T
ZMUC 00101374	3	F	52+0+T	8,1	?13			B	B	B			B	B	B			B	B	B			B	B	B			B	B	B			B	B		B	B			T
ZMUC 00101372	2	jF	53+0+T	7,2	?10				B	B	B			B	B	B			B	B	B			B	B			B	B	B			B	B						T
ZMUC 00101496		jF	51+2+T	6,4	12!				B	B				B	B	B		B	B	B			B	B	B	b	B	B	B			B	B			B	B	a	a	T
ZMUC 00101337		M	52+T+0	10,0	?16				B	B				B	B			B	B	B			B	B				B	B			B	B			b			T	
ZMUC 00101509		M	52+0+T	11,0	?				B	B				B	B			B	B	B			B	B			B	B	B			B	B						T	
ZMUC 00101495		M	52+0+T	10,2	?				B	B				B	B			B	B	B			B	B	B			B	B				B						T	
ZMUC 00101344		F	52+0+T	11,8	?16+									b					b					b					b				b						T	
ZMUC 00101374	1	F	52+0+T	10,8	?16		B	B	B			B	B	B			B	B	B			B	B	B				B	B			B	B						T	
ZMUC 00101374	2	jF	52+0+T	7,7	?15			B	B				B	B	B			B	B			B	B	B			B	B			B	B	B		B	B			T	
ZMUC 00101372	3	M	52+0+T	9,4	?						b			b	b						b			b	b		b	b	b			b	b						T	
ZMUC 00101372	4	jF	52+0+T	8,3	?14+										B	B			B	B	B			B	B	B		B	B	B			B	B						T	
ZMUC 00101343		jF	49+3+T	5,2	?11				B	B	B			B	B	B			B	B	B			B	B	B			B	B	B		B	B	B	a	a	a	T	
ZMUC 00101338	1	jF	51+0+T	7,2	?14		B	B	B			B	B	B			B	B	B			B	B	B			B	B			B	B			b			T		

Collection no.	Spm no.	Sex	Rings	Ø (mm)	RO	No. of podous rings																																			
						20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	
ZMUC 00101338	2	j?F	51+0+T	9,5	?15		B	B	B			B	B	B			B	B	B			B	B	B			B	B			B	B			B	B		T		
ZMUC 00101373		M	51+0+T	9,8	?				B	B				B	B			B	B			B	B	B			B	B			B	B						T		
ZMUC 00101338	3	M	51+0+T	9,8	?16+			B	B			B	B	B			B	B	B			B	B			B	B	B		B	B		b	b				T		
ZMUC 00101339		F	51+0+T	11,3	?17				?	B			B	B	B			B	B				B	B			B	B			?	B						T		
ZMUC 00101497	1	jF	51+0+T	8,1	?			B	B	B				B	B	B		B	B	B			B	B		B	B	B			B	B		B	B			T		
ZMUC 00101497	2	jF	50+1+T	6,1	12!				b					B	B		B	B	B			B	B			B	B	B			B	B					a	T		
ZMUC 00101493		jM	45+3+T	4,7	11			B	B			b	B	B			B	B				B	B			B	B			B	B	a	a	a	T					
ZMUC 00101340	1	j	34+5+T	2,5	5				B	B			B	B	B			B	B	B	a	a	a	a	a	T														
ZMUC 00101341		j	34+5+T	2,5	5			B	B	B				B	B				B	B	a	a	a	a	a	T														
ZMUC 00101342	1	j	34+5+T	2,5	5				B	B				B	B				B	B	a	a	a	a	a	T														
ZMUC 00101340	2	j	33+5+T	2,5	5				B	B			B	B			B	B	B	a	a	a	a	a	T															
ZMUC 00101342	2	j	29+5+T	1,9	4			B	B					B	B	a	a	a	a	a	T																			

Table 4. Body ring formulae in 26 specimens of *Sagmatosreptus strongylopygus*. Formulae in **bold** on a yellow background were observed, other formulae were inferred from colour patterns.

Collection no.	Spm no.	Sex	Body ring formulae							
			3RO	4RO	5R0	5R0+1	5R0+2	5RO+3	5R0+4	5RO+5
ZMUC 00101372	1	F		30+5+T	35+5+T	40+4+T	44+4+T	48+?+T	?	**53+0+T**
ZMUC 00101374	3	F	24+5+T	29+5+T	34+5+T	39+5+T	44+4+T	48+3+T	51+?+T	**53+0+T**
ZMUC 00101372	2	jF	25+5+T	30+5+T	35+4+T	39+5+T	44+4+T	48+?+T		**53+0+T**
ZMUC 00101496		jF	24+6+T	30+4+T	34+5+T	39+4+T	43+4+T	47+4+T	**51+2+T**	53+?0+T
ZMUC 00101337		M	24+5+T	29+5+T	34+4+T	38+5+T	43+4+T	47+3+T	50+?+T	**52+0+T**
ZMUC 00101509		M	24+5+T	29+5+T	34+4+T	38+5+T	43+4+T	47+?+T	?	**52+0+T**
ZMUC 00101495		M	24+5+T	29+5+T	34+5+T	39+4+T	43+4+T	47+?+T	?	**52+0+T**
ZMUC 00101344		F		28+5+T	33+5+T	38+5+T	43+4+T	47+?+T	?	**52+0+T**
ZMUC 00101374	1	F	23+5+T	28+5+T	33+5+T	38+5+T	43+4+T	47+?+T	?	**52+0+T**
ZMUC 00101374	2	jF	23+6+T	29+4+T	33+5+T	38+4+T	42+5+T	47+3+T	50+2?+T	**52+0+T**
ZMUC 00101372	3	M	25+4+T	29+6+T	35+4+T	39+4+T	43+4+T	47+?+T	?	**52+0+T**
ZMUC 00101372	4	jF		30+5+T	35+5+T	40+4+T	44+4+T	48+?+T	?	**52+0+T**
ZMUC 00101343		jF	25+5+T	30+5+T	35+5+T	40+5+T	45+4+T	**49+3+T**	52+0?+T	
ZMUC 00101339		F	24+5+T	29+4+T	33+5+T	38+4+T	42+4+T	46+?+T		**51+0+T**
ZMUC 00101338	1	jF	23+5+T	28+5+T	33+5+T	38+4+T	42+4+T	46+3+T	49+2?+T	**51+0+T**
ZMUC 00101338	2	j?F	23+5+T	28+5+T	33+5+T	38+4+T	42+4+T	46+4+T	50+1?+T	**51+0+T**
ZMUC 00101373		M	24+5+T	29+4+T	33+5+T	38+4+T	42+4+T	46+?+T		**51+0+T**
ZMUC 00101338	3	M	23+5+T	28+5+T	33+4+T	37+5+T	42+3+T	45+3+T	48+?+T	**51+0+T**
ZMUC 00101497	1	jF	24+6+T	30+4+T	34+4+T	38+4+T	42+4+T	46+3+T	49+?+T	**51+0+T**
ZMUC 00101497	2	jF	23+6+T	29+4+T	33+4+T	37+5+T	42+4+T	46+?+T	**50+1+T**	51+0?+T
ZMUC 00101493		jM	23+5+T	28+4+T	32+5+T	37+4+T	41+4+T	**45+3+T**	48+?+T	
ZMUC 00101340	1	j	24+5+T	29+5+T	**34+5+T**	39+?+T				

Collection no.	Spm no.	Sex	Body ring formulae							
			3RO	4RO	5R0	5R0+1	5R0+2	5RO+3	5R0+4	5RO+5
ZMUC 00101341		j	24+5+T	29+5+T	**34+5+T**	39+?+T				
ZMUC 00101342	1	j	24+5+T	29+5+T	**34+5+T**	39+?+T				
ZMUC 00101340	2	j	24+4+T	28+5+T	**33+5+T**	38+?+T				
ZMUC 00101342	2	j	23+6+T	**29+5+T**	34+?+T					

reach far higher numbers of podous body rings and may therefore not be directly compared with the present findings.

The number of apodous rings: developmental patterns

In the course of anamorphosis of juliformian millipedes, the number of apodous rings usually reaches a maximum early in development and thereafter decreases monotonically (reaching 0 in hemianamorphic species like *S. strongylopygus*), i.e., a unimodal distribution of numbers of apodous rings over developmental time (Enghoff et al. 1993: 202 ff). Looking at the numbers of inferred (and observed, in the case of the anamorphic specimens) apodous rings (Table 6) we find disagreement with the unimodal model in half of the 20 specimens in which four or more numbers of apodous body rings could be inferred/observed.

Deviations from the unimodal pattern have been observed in a few other millipede species belonging to the family Julidae (order Julida) (Sahli 1969, Saudray 1961). Non-unimodal patterns of body ring increments may be the results of the regulatory mechanism described from *Narceus annularis* (Rafinesque, 1820) (order Spirobolida, family Spirobolidae) by Berns and Keeton (1968a, b). These authors found that when anamorphic specimens of *N. annularis* were starved, they added fewer body rings per moult than well-fed individuals during the first moults, but that they compensated by adding more body rings per moult than well-fed individuals during the last part of anamorphosis. Berns and Keeton did not give information for individual specimens.

Platydesmus spp.

Quite complicated and irregular trans-segmental colour patterns occur in several species of the order Platydesmida. For example, Pocock (1910) described and illustrated several Central American *Platydesmus* species (fam. Platydesmidae) with such patterns (Fig. 5):

Platydesmus perpictus Pocock, 1910, has about seven multi-pleurotergite pattern elements, with limits between elements at pleurotergites 15, 23, 27, 32, 37, 42, 45 and

Table 5. Inferred and observed body ring formulae in *Sagmatostreptus strongylopygus.* The number of specimens with each formula is shown in parentheses after the formula, observed formulae indicated with underlined numbers. The last column shows the range of podous and apodous body rings inferrred/observed for each RO stadium.

Stadium									Range
3 RO	23+5+T (5)	23+6+T (3)	24+4+T (1)	24+5+T (9)	24+6+T (2)	25+4+T (1)	25+5+T (2)		23-25+4-6
4 RO	28+4+T (1)	28+5+T (6)	29+4+T (4)	29+5+T (7+1)	29+6+T (1)	30+4+T (2)	30+5+T (4)		28-30+4-6
5 RO	32+5+T (1)	33+4+T (2)	33+5+T (7+1)	34+4+T (3)	34+5+T (3+3)	35+4+T (2)	35+5+T (3)		32-35+4-5
5 RO+1	37+4+T (1)	37+5+T (2)	38+4+T (6)	38+5+T (4)	39+4+T (3)	39+5+T (2)	40+4+T (2)	40+5+T (1)	37-40+4-5
5 RO+2	41+4+T (1)	42+3+T (1)	42+4+T (6)	42+5+T (1)	43+4+T (7)	44+4+T (4)	45+4+T (1)		41-45+3-5
5 RO+3	45+3+T (1+1)	46+3+T (2)	46+4+T (1)	47+3+T (2)	47+4+T(1)	48+3+T (1)	49+3+T (1)		45-49+3-4
5 RO+4	50+1+T (1+1)	51+2+T (1)							50-51+1-2
epimorphic spms	51+0+T (6)	52+0+T (8)	53+0+T (3)						51-53+0

Table 6. Numbers of apodous body rings in specimens of *Sagmatostreptus strongylopygus* in which at least 4 successive numbers could be inferred or observed.

Collection no.	Spm no.	3RO	4RO	5RO	5RO+1	5RO+2	5RO+3	5RO+4	Unimodality
ZMUC 00101372	1		5	5	4	4			yes
ZMUC 00101374	3	5	5	5	5	4	3		yes
ZMUC 00101372	2	5	5	4	5	4			NO
ZMUC 00101496		6	4	5	4	4	4		NO
ZMUC 00101337		5	5	4	5	4	3		NO
ZMUC 00101509		5	5	4	5	4			NO
ZMUC 00101495		5	5	5	4	4			yes
ZMUC 00101344			5	5	5	4			yes
ZMUC 00101374	1	5	5	5	5	4			yes
ZMUC 00101374	2	6	4	5	4	5	3		NO
ZMUC 00101372	3	4	6	4	4	4			yes
ZMUC 00101372	4		5	5	4	4			yes
ZMUC 00101343		5	5	5	5	4	3		yes
ZMUC 00101339		5	4	5	4	4			NO
ZMUC 00101338	1	5	5	5	4	4	3		yes
ZMUC 00101338	2	5	5	5	4	4	4		yes
ZMUC 00101373		5	4	5	4	4			NO
ZMUC 00101338	3	5	5	4	5	3	3		NO
ZMUC 00101497	1	6	4	4	4	4	3		yes
ZMUC 00101497	2	6	4	4	5	4		1	NO
ZMUC 00101493		5	4	5	4	4	3		NO

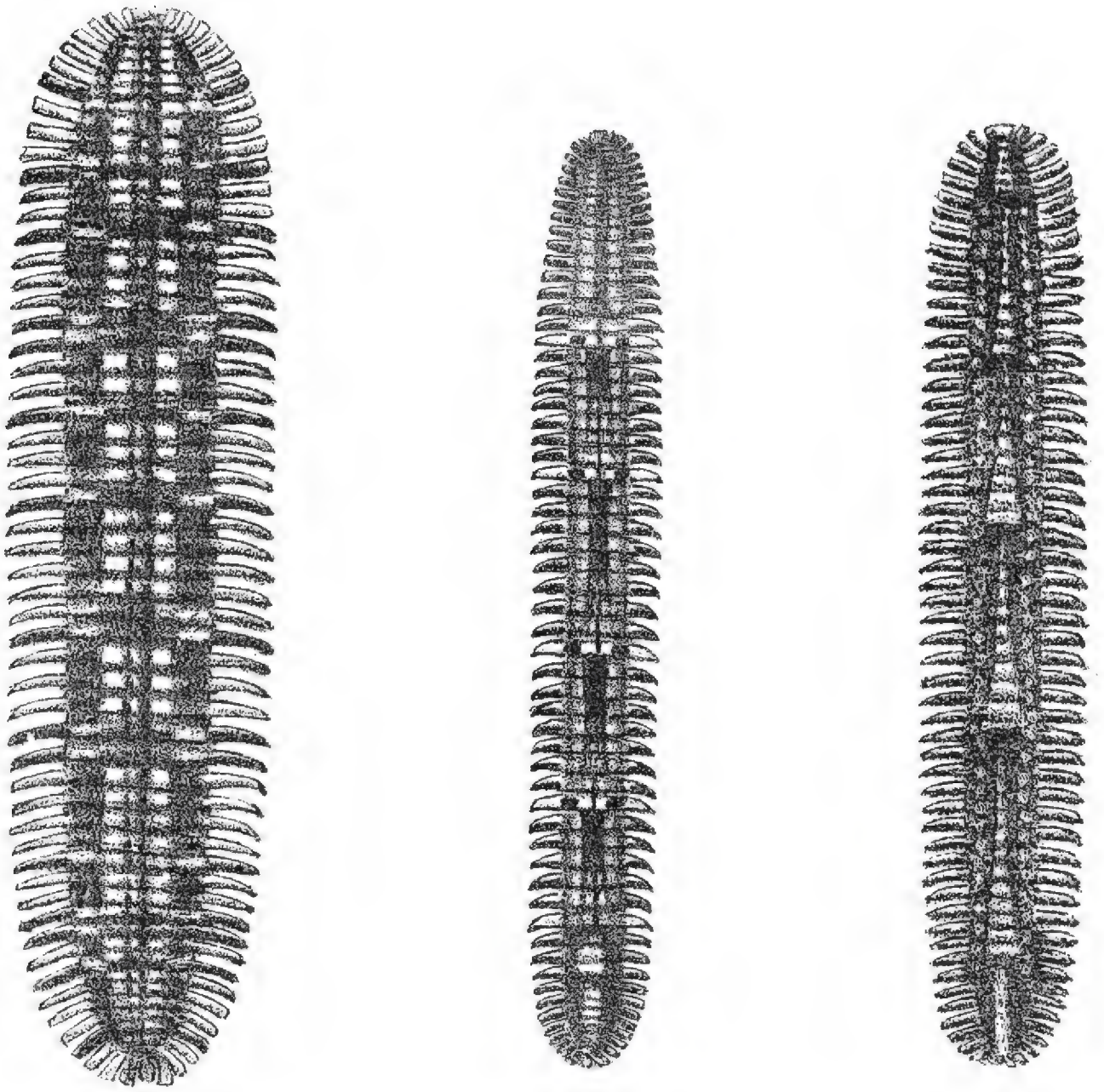

Figure 5. Left: *Platydesmus perpictus* Pocock, 1910, Middle: *P. analis* Pocock, 1910, Right: *P. triangulifer* Pocock, 1910. From Pocock (1910).

47 (as far as can be judged from the illustration, Fig. 5A, the same reservation applies to the following two species).

Platydesmus analis Pocock, 1910, has six multi-pleurotergite pattern elements. For this species, Pocock (1910) gave the limits: "....with a yellow spot in the centre of the fourteenth, twenty-second, thirty-second, fortieth, forty-sixth and fiftieth segments, the keels of these same segments yellow).

Platydesmus triangulifer Pocock, 1910, has six multi-pleurotergite pattern elements, according to Pocock (1910): "...pale median band, which is not of even thickness throughout but is broken up at fairly regular intervals into six elongate triangular expansions, being broadest upon the sixth, fifteenth, twenty-fourth, thirty-fourth, forty-fifth, and fifty-second segments".

The patterns in these *Platydesmus* species are summarised in Table 7.

Thanks to Paul Marek, I have become aware of a striking photo by Steve Taylor, featuring a group of platydesmids from Costa Rica (Fig. 6, the photo is also available at http://www.flickr.com/photos/ceuthophilus/147312880.

Table 7. Transsegmental colour patterns in *Platydesmus* species described by Pocock (1910). A: Entries are limits between pattern elements, given as pleurotergite numbers (counted from the head end). An attempt has been made to place pleurotergite numbers corresponding to the same stadium in the same column. B: entries are differences, expressed as no. of pleurotergites, between one limit and the one in front of it.

A:										
P. perpictus		15	23	27	32	37	42	45	47	
P. analis		14	22		32		40	46		50
P. triangulifer	6	15	24		34			45		52
B:										
P. perpictus			8	4	5	5	5	3	2	
P. analis			8	10	8	6	4			
P. triangulifer		9	9	10	11	7				

There are 8 adult individuals on the photo. Each has 4–6 transsegmental pattern elements. Each element consists of a triangular light marking on each side of the midline, each triangle covering 3–5 pleurotergites and becoming narrower at its posterior end. The elements are separated by 2–3 unmarked pleurotergites. The anterior limit of each element is sharply marked. The anterior end of the specimens is difficult to identify on most specimens, so the absolute tergum numbers may be wrong by one or two. This is, however, less important – the important thing is the nature of the periodicity. Table 8 summarises the patterns in these specimens.

Beautiful photos of a *Platydesmus* sp. from Guatemala are available at http://www.nadiplochilo.com/oplatydesmida.html but the colour pattern could not be analysed.

Brachycybe picta

Gardner (1975) described a new species of the other platydesmidan family, Andrognathidae, from California, *Brachycybe picta*, describing a trans-segmental colour pattern: "area of dorsum over body cylinder generally tan colored, with five brown spots on the mesal area in regularly spaced groups of four to five body segments each". Other species of *Brachycybe* don't have such a pattern, and Shelley et al. (2005) say nothing about the colour pattern although they record new material of *B. picta*.

SE Asian andrognathids (*?Pseudodesmus* spp.)

Two variegated species of Andrognathidae have been described from Vietnam and Laos: *Sumatronium variegatum* Attems, 1938b, and *S. persimile* Attems, 1953. Generic concepts in SE Asian andrognathids are not at all settled and are subject of ongoing research by Peter Decker – for the time being I will refer all concerned species to the

Figure 6. Unidentified platydesmids from Costa Rica, P. Marek & J.E. Bond leg. Adult specimens code: Left top: **1** left bottom **2** middle top **3** middle middle **4** middle bottom **5** right top **6** right middle **7** right bottom **8** cf. text and table 8 S. Taylor phot. See also http://www.flickr.com/photos/ceuthophilus/147312880.

Table 8. Trans-segmental colour patterns in unidentified platydesmid from Costa Rica (Fig. 5). A: Entries are limits between pattern elements, given as the number of the anteriormost pleurotergite in each pattern element. An attempt has been made to place pleurotergite numbers corresponding to the same stadium in the same column. B: entries are differences, expressed as no. of pleurotergites, between one limit and the one in front of it or, in other words, numbers of pleurotergites constituting one colour pattern element.

A:								
specimen 1		12	19	26		33		
specimen 2	8	16	21		29			
specimen 3		14	21		29		37	
specimen 4		14	20		27	33		
specimen 5		14	20	25	31		37	42
specimen 6	7	15	20	26		33		
specimen 7	7	14	21		28	35		
specimen 8	7	15	22		28	35		40
B:								
specimen 1			7	7		7		
specimen 2		8	5		8			
specimen 3			7		8			
specimen 4			6		7	6		
specimen 5			6	5	6		6	5
specimen 6		8	5	6		7		
specimen 7		7	7		7	7		
specimen 8		8	7		6	7		5

genus *Pseudodesmus* (the oldest available genus name based on a SE Asian species of this group). Recently, a specimen with a similar colour pattern has been photographed in Malaysia by P. Pimvichai (Fig. 7).

I have examined a sample of *P.* cf. *variegatus* from Laos. The dorsal colour pattern of adults is highly complicated and irregular (Fig. 8). The general background is greyish brown, but is interrupted by four types of coloured components:

Paratergal spots: clear lateral yellowish spots which occupy the middle of a paratergite (lateral 'wing'). These spots occur in groups, and the posteriormost spot in each group is usually enlarged and clearly marks the limit of the pattern element. (This is in contrast to the patterns in *Platydesmus* where the anterior limit of the pattern elements is clearly demarcated.)

Less well-defined yellowish brown spots which occupy an area roughly corresponding to the basal third of the paratergites and is delimited vis-a-vis the lateral spots and vis-a-vis the paramedian tubercles by a small blackish area. These spots occur on all pleurotergites.

Pale tubercular spots: clear paramedian yellowish spots which occupy the two consecutive paramedian tubercles on a pleurotergite. These spots occur in an irregular pattern along the body, interrupted by the belowmentioned black spots.

Dark tubercular spots: paramedian black spots which occupy the two consecutive paramedian tubercles on a pleurotergite.

Paratergal and tubercular spots show asymmetrical patterns, see, e.g., Table 9. Analysis of the pattern shown in Table 9 reveals, however, that in spite of the apparent chaos there are some regularities:

There is a strong tendency for the often enlarged posteriormost lateral spot in a group to occur on both sides of the same pleurotergite, in casu pleurotergites nos. (14), 22, 28, 37, 44, 47, [54], 58, (61) where numbers in round parentheses indicate 'groups' of one spot, and the number in square brackets indicates asymmetry.

Pale tubercular spots (72 instances) are more frequent than dark ones (40 instances).

Pleurotergites with two dark tubercular spots are infrequent: 4 instances, compared with 21 instances of double-white and 31 instances of mixed colours.

There is a highly significant correlation (P= 5,33086E-13, chi2-test, 2×2 matrix, Table 10) between presence of a lateral spot and the colour of the tubercular spot on the same side of the same pleurotergite.

(Follows almost automatically from previous): There is a tendency for the tubercular sports to be pale on both sides on the posteriormost pleurotergite of each lateral group. Thus, both tubercular spots are pale on pleurotergites 14, 22, 28, 37, 44, 47, 58 and 61, i.e. on all the pleurotergites mentioned in the previous statement except the dubious pleurotergite 54. The preponderance is highly significant (P ~0.0005, chi2-test, 2×2 matrix).

Table 11 shows colour pattern statistics for four specimens. It is seen that the pattern regularities found in the specimens tabulated in Table 9 are quite general although the female with 63 pleurotergirtes has more black tubercular spots than the others. Table 12 shows the position of the limits between pattern elements (= position of enlarged posteriormost lateral spots in a group) in all ten specimens in the sample, and the distance (no. of pleurotergites) between element limits. On specimens with

Figure 7. Unidentified platydesmid from Malaysia. P. Pimvichai phot.

Figure 8. *Pseudodesmus* cf. *variegatus* from LAOS, Vientiane Prov., Phou Khao Khouay, N 18, 20,369', E 102, 48,523', 7–800 m, 28–31.v.2008, A. Solodovnikov & J. Pedersen leg. (ZMUC), posterior part of body. Length of fragment 23 mm.

< 55 pleurotergites, which are generally much paler, no lateral spots are visible, but the irregular distribution of black and white tubercular spots is clear. Limits between pleurotergite series on these specimens were identified by locating the posterior limit of (series of) double white tubercular spots.

Interpretation of patterns in Platydesmida

Since the colour patterns of *Centrobolus vastus* var. *sexfasciatus* and *Sagmatostreptus strongylopygus* could be interpreted as reflecting anamorphosis, it is natural to con-

Table 9. Occurrence of lateral and paramedian colour components along the body of a *Pseudodesmus* cf. *variegatus* female with 65 pleurotergites (excluding telson) ZMUC 00101498/A. Occurrence is indicated by "+" for the lateral component (yellowish spot on paratergum), and by black and white squares (□ and ■, for pale and dark spots, respectively) for the paramedian tubercular spots. ++ indicates the posterior, enlarged lateral spot in a group.

	Lateral left	**Paramedian tubercle left**	**Paramedian tubercle right**	**Lateral right**
Tergite no.				
1				
2				
3				
4				
5				
6		□	□	
7		□	■	
8		■	□	
9		□	■	
10		■	□	
11		□	■	
12		■	□	+
13		□	□	
14	+	□	□	+
15		■	□	
16		■	□	
17		■	□	+
18		■	□	
19	+	□	■	
20		■	□	+
21	+	□	□	+
22	+	□	□	++
23		■	□	
24	+	□	■	
25	+	□	■	
26	+	□	■	
27		□	□	+
28	++	□	□	++
29		■	■	
30		■	■	
31		□	■	
32	+	□	■	
33		■	□	+
34	+	□	□	+
35	+	□	■	
36	+	□	□	+
37	++	□	□	++
38		■	■	

	Lateral left	Paramedian tubercle left	Paramedian tubercle right	Lateral right
39		■	□	+
40	+	□	■	
41	+	□	□	+
42	+	□	□	+
43	+	□	□	+
44	++	□	□	++
45	+	□	■	
46	+	□	□	+
47	++	□	□	++
48		■	■	
49		■	□	
50	+	□	■	+
51	+	□	■	
52	+	□	□	
53	+	□	□	+
54	++	□	■	
55		■	□	
56	+	□	■	
57	+	□	□	+
58	+	□	□	+
59		■	■	
60		■	□	
61	+	□	□	+
62				
63				
64				
65				

Table 10. Correlation between colour of tubercular spots and presence of lateral spots in a *Pseudodesmus* cf. *variegatus* female (ZMUC 00101498/A).

	Tubercular spot white	Tubercular spot black
Lateral spot present	53	1
Lateral spot absent	19	39

sider whether this might also be the case for the platydesmids and andrognathids. The little that is known about anamorphosis in Platydesmida is almost exclusively due to Murakami (1962ab, 1963) who made a detailed study of the andrognathid *Brachycybe (=Bazillozonium) nodulosa* (Verhoeff, 1935). Of particular importance in the present context is his diagram (Murakami 1963) here shown as Fig. 9, in which the numbers of pleurotergites in each stadium are shown, together with observed pathways between stadia.

Table 11. Colour pattern statistics for four specimens of *Pseudodesmus* cf. *variegatus.*

	♀ 65 pleurotergites	♂ 63 pleurotergites	♀ 63 pleurotergites	♂ 56 pleurotergites
Pattern on tergites	6–61	7–59	6–61	6–50
White/black tubercular spots	72/40	62/44	55/57	54/36
Double-black/double-white/mixed pair of tubercular spots	4/21/31	4/21/28	15/13/28	8/17/20
White/black tubercular spot on hemitergite with lateral spot	53/1	47/0	41/1	37/0
White/black tubercular spot on hemitergite without lateral spot	19/39	15/44	14/56	17/36
P (chi^2, 2×2 matrix) for values in rows 4 and 5	5,33086E-13	9,85096E-15	1,79343E-15	9,67137E-11

Table 12. Position of enlarged posteriormost lateral spots in a group of spots in ten specimens of Pseudodesmus cf. variegatus ZMUC 00101498. (14), 22, 28, 37, 44, 47, [54], 58, (61) where symbols in round parentheses indicate 'groups' of one spot, symbol in square brackets indicates asymmetry (spot only present on one side).

A:									
♀ 65 tergites	(14)	22	28	37	44	47	[54]	58	(61)
♂ 63 tergites		19	26	34	42	49	55	59	
♀ 63 tergites	(12)	18	25	33	41	48	54	58	(61)
♂ 56 tergites	(14)	20	28	36	43	50			
♂ 46 tergites	13	20	27	33	41				
♂ 47 tergites	13	19	27	35					
♀ 44 tergites	13	21	28	35					
j♂ 45 tergites	13	19	25	33	39				
♀ 44 tergites	13	18	24	30					
♀ 40 tergites	13	19	25	34					
B:									
♀ 65 tergites		8	6	9	7	3	7	4	3
♂ 63 tergites			7	8	8	7	6	4	
♀ 63 tergites		6	7	8	8	7	6	4	3
♂ 56 tergites		6	8	8	7	7			
♂ 46 tergites		7	7	6	8				
♂ 47 tergites		6	8	8					
♀ 44 tergites		8	7	8					
j♂ 45 tergites		6	6	8	6				
♀ 44 tergites		5	6	6					
♀ 40 tergites		6	6	9					

The anamorphosis of *B. nodulosa* is characterized by great variability:

4–8 pleurotergites are added between stadia I and II
3–8 pleurotergites are added between stadia II and III
4–8 pleurotergites are added between stadia II and IV
4–8 pleurotergites are added between stadia IV and V
3–8 pleurotergites are added between stadia V and VI
3–8 pleurotergites are added between stadia VI and VII
3–8 pleurotergites are added between stadia VII and VIII

The wide range of pleurotergal increments between stadia is consistent with the wide range of the numbers of pleurotergites which constitute a colour pattern element in the patterned platydesmids and andrognathids studied here. In other words, the colour pattern of an individual may well reflect the anamorphic pathway it has followed.

Siphonocryptus zigzag

The holotype and only known specimen of *Siphonocryptus zigzag* Enghoff, 2010 (order Siphonocryptida) has 32 pleurotergites and a serial colour pattern consisting of three elements covering pleurotergites 14–20, 21–27 and 28–32, respectively. The distances between colour element borders correspond to seven pleurotergites which lies within the rather wide range of distances seen in Platydesmida. However, considering the low number of pleurotergites in *Siphoncryptus* adults, it appears unlikely that consecutive anamorphic stadia would differ by as much as seven pleurotergites. Nothing is known about anamorphosis of the genus *Siphonocryptus* (the fragmentary information given by Enghoff et al. (1993) on *S. canariensis* Loksa, 1967 actually pertains to the genus *Hirudicryptus,* cf. Enghoff and Golovatch 1995).

Australeuma and *?Schedotrigona* species

In several species of the Australian metopidiotrichid genus *Australeuma* (order Chordeumatida), there is a pronounced trans-segmental pattern. For example Shear and Mesibov (1997) described their new species *A. mauriesi* as follows: "Colour pale tan, paranota of segments 3–5 dark brown; other segments with pattern varying in groups of five segments, the first segment in the group having small brown patches near the midline, these becoming larger and more distinct posteriorly and progressively closer to the paranotal bases in succeeding segments of the group, the overall effect being a light-coloured animal with five of six chevron-shaped dark markings." Photographs of two *Australeuma* species with trans-segmental patterns are available at http://www.polydesmida.info/tasmanianmultipedes. Analysis of the photos shows that the periodicity of the colour pattern is not invariably by five pleurotergites – in several cases it is four.

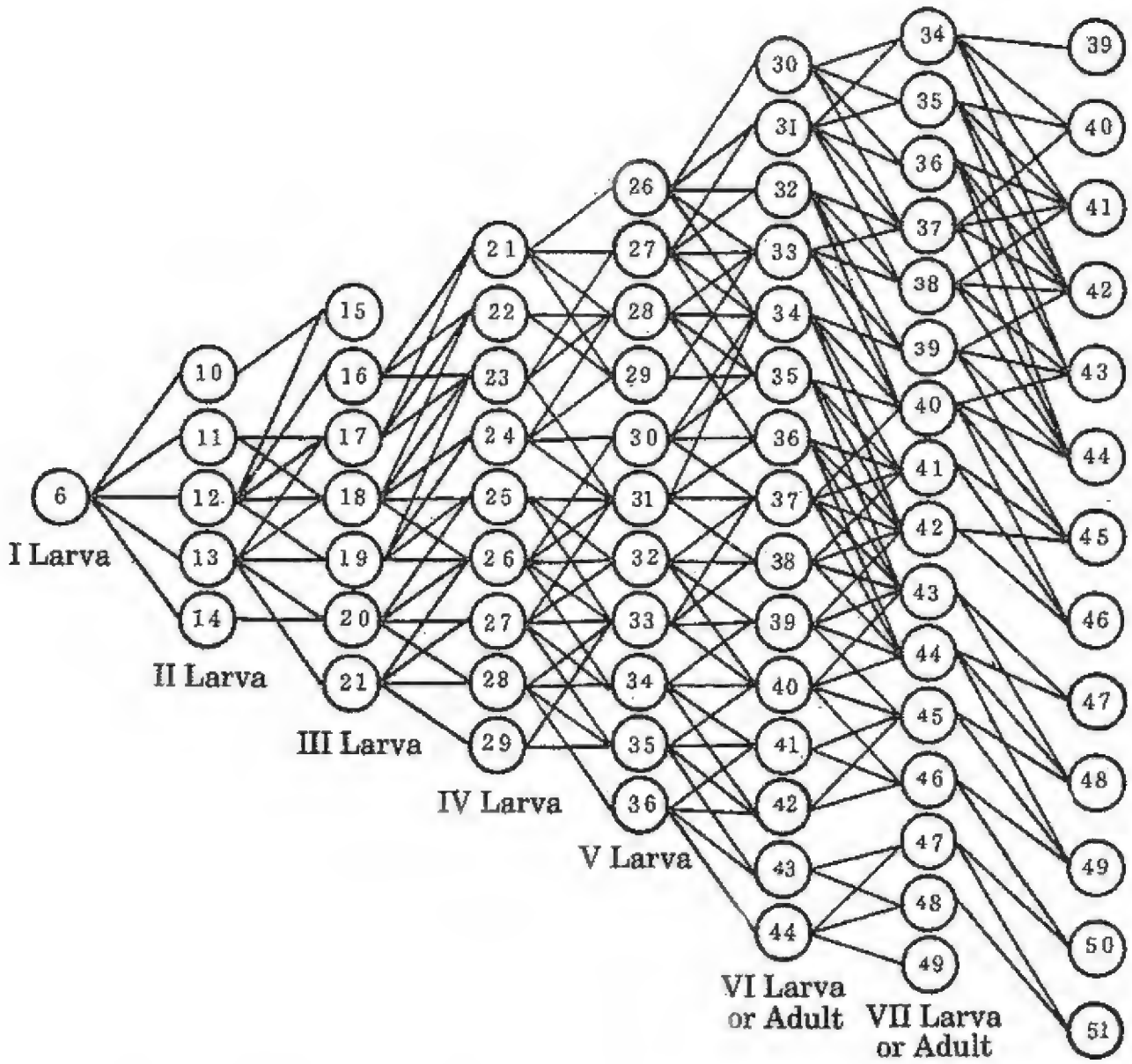

Figure 9. Anamorphosis in *Brachycybe (=Bazillozonium) nodulosa* (Verhoeff, 1935). The diagram shows the numbers of pleurotergites in the anamorphic stadia, as well as observed pathways between stadia. From Murakami (1963).

Fig. 10 shows two unidentified specimens of Chordeumatida from New Zealand (A. Solodovnikov and L. Vilhelmsen leg, ZMUC). They probably belong to the genus *Schedotrigona* (fam. Metopidiothricidae) which is the only known genus of Chordeumatida in New Zealand (Mauriès 1978) The specimen from Lake Gunn is a subadult male; it is generally dark brown with a paler dorsum and with dorsolateral pale spots on pleurotergites 3–6, 7–8, 10–11, 14–15, 18–19, 22–23, and 26–27. The specimen from Mt. Burns is a subadult female; it is generally whitish yellow, but with dorsal pairs of dark spots on pleurotergites 1–11, 15, 19, 23, 27. In both specimens there are limits between pattern elements at pleurotergites 11, 15, 19, 23, and 27, i.e., a periodicity of four pleurotergites.

No species of Metopidiotrichidae has been studied with regard to postembryonic development, but in related families, the maximal number of apodous pleurotergites is 4 (Enghoff et al. 1993). The colour pattern seen in ?*Schedotrigona* would thus be consistent with an 'anamorphic' basis, whereas that in *Australeuma* is partly in conflict with such an explanation.

Figure 10. Two species of unidentified Chordeumatida from New Zealand (A. Solodovnikov & L. Vilhelmsen leg., ZMUC). Top: subadult male from South Island, Fiordland/Otago District, Lake Gunn, 44°51.500 S, 168°06.086 E, 500 masl, mixed conifer/broadleaf/beech forest, sifted leaf litter, 25.i.2011. Bottom: subadult female from South Island, Fiordland District, W slopes of Mt. Burns (W of Monowai), 45°44.808 S, 167°23.109 E, 900–950 masl, beech forest, in leaf litter and under logs, 23.i.2011. N. Akkari phot. Scales 1 mm.

Concluding remarks

The colour patterns described above remain exceptions among millipedes. Whereas an aposematic functon of the pattern appears obvious in *Centrobolus vastus* var. *sexfasciatus* and *Sagmatostreptus strongylopygus*, this is probably not the case for the patterned species of Platydesmida, Siphonocryptida and Chordeumatida. In fact, they may rather have

a camouflaging function – in particular the asymmetrical pattern seen in *Pseudodesmus* cf. *variegatus* might help to dissolve the contour of the animal (I. Tuf, personal communication). The idea that the patterns reflect postembryonic development – anamorphosis – appears well-founded for *Centrobolus vastus* var. *sexfasciatus* and *Sagmatostreptus strongylopygus* and reasonable for the species of Platydesmida and ?*Schedotrigona*. For *Siphonocryptus zigzag* and *Australeuma* spp. this explanation probably does not apply.

Acknowledgements

Specimens were made available by Didier VandenSpiegel, Alexey Solodovnikov, Lars Vilhelmsen and Jan Pedersen. Guido Coza, Paul Marek and Piyatida Pimvichai gave access to photos of live animals. Nesrine Akkari and Nicolas Ioannou provided photos of preserved specimens. Richard Hoffman kindly agreed to help to make the genus name *Sagmatostreptus* available. Peter Decker provided insight into the SE Asian andrognathids. Ivan Tuf suggested a possible cryptic function of the asymmetrical pattern in *Pseudodesmus* cf. *variegatus*. I extend my thanks to all these persons.

References

Attems C (1938a) Myriapoda 3. Polydesmoidea II. Fam. Leptodesmidae, Platyrhachidae, Oxydesmidae, Gomphodesmidae. Das Tierreich 69: i-xxviii + 1–487.

Attems C (1938b) Die von Dr. C. Dawydoff in Französisch Indochina gesammelten Myriopoden. Mémoires du Muséum national d'Histoire naturelle, Nouvelle série 6: 187–321.

Attems C (1953) Myriopoden von Indochina. Expedition von C. Dawydoff (1938–1939). Mémoires du Muséum national d'Histoire naturelle, Série A (Zoologie) 5,3: 133–230.

Berns MW, Keeton WT (1968a) Effects of semi-starvation on growth and morphogenesis during the larval stages of a common milliped, *Narceus annularis* (Raf.). Biological Bulletin 135: 454–465.

Berns MW, Keeton WT (1968b) Regulation of segment-building during the postembryonic development of a common milliped. Science 161: 590–592.

Dhaenens M, VandenSpiegel D (2006) Contribution to the study of the post-embryonic development and reproduction of the African millipede *Epibolus pulchripes* (Gerstäcker, 1873) (Diplopoda, Pachybolidae). Belgian Journal of Zoology 136: 43–51.

Eisner T, Alsop D, Hicks K, Meinwald J (1978) Defensive Secretions of Millipedes. In: Bettini S (Ed) Arthropod Venoms. Handbook of Experimental Pharmacology, vol. 48. Springer-Verlag, Berlin, New York, 41–72.

Enghoff H (2010) A new strikingly coloured species of *Siphonocryptus*, sixth of its order (Diplopoda: Siphonocryptida). Zootaxa 2681: 66–68.

Enghoff H, Dohle W, Blower JG (1993) Anamorphosis in millipedes (Diplopoda) – the present state of knowledge with some developmental and phylogenetic considerations. Zoological Journal of the Linnean Society 109: 103–234.

Enghoff H (2011) East African giant millipedes of the tribe Pachybolini (Diplopoda, Spirobolida, Pachybolidae). Zootaxa 2753: 1–41.

Enghoff H, Golovatch SI (1995) A revision of the Siphonocryptidae (Diplopoda, Polyzoniida). Zoologica Scripta 24: 29–41.

Enghoff H, Sutcharit C, Panha S (2007) The shocking pink dragon millipede, *Desmoxytes purpurosea*, a colourful new species from Thailand (Diplopoda: Polydesmida: Paradoxosomatidae). Zootaxa 1563: 31–36.

Gardner M (1975) ("1974") Revision of the millipede family Andrognathidae in the Nearctic region. Memoirs of the Pacific Coast Entomological Society 5: 1–61.

Gillon D, Gillon Y (1982) Croissance post-embryonnaire des principales espèces d'lules (Myriapodes: Diplopodes) de milieu Soudanien au Sénégal. Revue d'Écologie et de Biologie du Sol 19: 277–288.

Hoess R (2000) Bestimmungsschlüssel für die *Glomeris*-Arten Mitteleuropas und angrenzender Gebiete (Diplopoda: Glomeridae). Jahrbücher des Naturhistorischen Museum Bern 13: 3–20.

Hoffman RL, Enghoff H (2011) A new genus for a colorful spirostreptid milliped from northeastern Tanzania (Diplopoda: Spirostreptida). Zootaxa 2903: 21–28.

Jeekel CAW (1958) Millipede miscellany – Part III. Beaufortia 5(51): 73–99.

Kime RD, Enghoff H (2011) Atlas of European millipedes (Class Diplopoda), volume 1, orders Polyxenida, Glomerida, Platydesmida, Siphonocryptidae, Polyzoniida, Callipodida, Polydesmida. Fauna Europaea Evertebrata 3, Pensoft, Sofia-Moscow, 282.

Korsós Z, Jenő K, Dávid M (2001) ("1999") Újabb adatok a *Polydesmus collaris* C.L. Koch, 1847 (Diplopoda: Polydesmida) Bakonyi elterjedéséhez. Folia Musei Historico-Naturalis Bakonyensis 18: 15–18.

Lawrence RF (1967) The Spiroboloidea (Diplopoda) of the eastern half of southern Africa. Annals of the Natal Museum 18: 607–646.

Levi HW (1965) An unusual case of mimicry. Evolution 19: 261–262.

Marek PE, Bond J (2006) Phylogenetic systematics of the colourful, cyanide-producing millipedes of Applachia (Polydesmida, Xystodesmide, Apheloriini) using a total evidence Bayesian approach. Molecular Phylogenetics and Evolution 41: 704–729.

Marek PE, Bond (2009) A Müllerian mimicry ring in Appalachian millipedes. Proceedings of the National Academy of Sciences 106: 9755–9760.

Mauriès J-P (1978) Le genre néo-zélandais *Schedotrigona* Silvestri, 1903: révision et place dans une nouvelle classification des craspedosomides (Myriapoda, Diplopoda, Craspedosomida). Bulletin du Muséum National d›Histoire Naturelle, Zoologie 351: 43–66.

Murakami Y (1962a) Postembryonic development of the common Myriapoda of Japan XI. Life history of *Bazillozonium nodulosum* Verhoeff (Corobognatha, Platydesmidae) 1. Zoological Magazine (Dobutsugaku Zasshi) 71: 250–255. [in Japanese]

Murakami Y (1962b) Postembryonic development of the common Myriapoda of Japan XI. Life history of *Bazillozonium nodulosum* Verhoeff (Colobognath,Platydesmidae) 2. Zoological Magazine (Dobutsugaku Zasshi) 71: 291–294. [in Japanese]

Murakami Y (1963) Postembryonic development of the common Myriapoda of Japan XI. Life history of *Bazillozonium nodulosum* Verhoeff (Colobognatha,Platydesmidae) 3. Zoological Magazine (Dobutsugaku Zasshi) 72: 40–47. [in Japanese]

Pocock RI (1910) Chilopoda and Diplopoda. Biologia Centrali-Americana. 217 pp., 15 plates.

Sahli F (1969) Contribution à l'étude du développement post-embryonnaire des Diplopodes Iulides. Annales Universitatis Saravensis mathematisch-naturwissenschafliche Fakultät 7: 1–154.

Saudray Y (1961). Recherches biologiques et physiologiques sur les Myriapodes Diplopodes. Mémoires de la Société Linnéenne de Normandie, nouvelle série, Zoologie 2: 1–126.

Schubart O (1966) Diplopoda III. South African Animal Life 12: 75–121.

Shear WA, Jones TH, Miras HM (2007) A possible phylogenetic signal in milliped chemical defenses: The polydesmidan milliped *Leonardesmus injucundus* Shelley & Shear secretes p-cresol and lacks a cyanogenic defense (Diplopoda, Polydesmida, Nearctodesmidae). Biochemical Systematics and Ecology 35: 838–842.

Shear WA, Mesibov R (1997) Australian chordeumatidan millipedes. III. A review of the millipede family Metopidiotrichidae Attems in Australia (Diplopoda: Chordeumatida). Invertebrate Taxonomy 11: 141–178.

Shelley RM, McAllister C, Tanabe T (2005) A synopsis of the milliped genus *Brachycybe* Wood, 1864 (Platydesmida: Andrognathidae). Fragmenta faunistica 48: 137–166.

Vitt LJ (1992) Lizard mimics millipede. National Geographic Research & Exploration 8: 76–95.

Wesener T (2009) Unexplored richness: discovery of 31 new species of Giant Pill-Millipedes endemic to Madagascar, with a special emphasis on microendemism (Diplopoda, Sphaerotheriida). Zootaxa 2097: 1–134.

Wesener T, Enghoff H, Hoffman RL, Wägele JW, Sierwald P (2009). Revision of the endemic giant fire millipedes of Madagascar, genus *Aphistogoniulus* (Diplopoda: Spirobolida: Pachybolidae). International Journal of Myriapodology 2: 15–52.

Wesener T, Schütte K (2010) Swarming behaviour and mass occurrences in the world's largest giant pill-millipede species, *Zoosphaerium neptunus*, on Madagascar and its implication for conservation efforts (Diplopoda: Sphaerotheriida). Madagascar Conservation and Development 5: 89–94.

Whitehead DR, Shelley RM (1992) Mimicry among aposematic Appalachian xystodesmid millipedes (Polydesmida, Chelodesmidea). Proceedings of the Entomological Society of Washington 94: 177–188.